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Westslope cutthroat trout size structure in the North Fork
Coeur d'Alene subbasin, Idaho

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WESTSLOPE CUTTHROAT TROUT SIZE STRUCTURE IN THE NORTH FORK COEUR D' ALENE SUBBASIN, IDAHO

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ABSTRACT

Understanding of diversity generating processes and spatial distribution of intraspecific phenotypic diversity is critical if species are to be conserved. An existing dataset including length data for westslope cutthroat trout (*Oncorhynchus clarki lewisi*) from the North Fork Coeur d' Alene River, northern Idaho, was analyzed to examine whether one aspect of intraspecific diversity, population size structure, was responsive to several environmental and spatial variables. In addition, relative behavior of different size structure metrics were examined. Length data from 53 streams distributed throughout the North Fork Coeur d' Alene River basin were collected one or more times during a 3-year period. Sixteen size structure metrics representing 5 qualitative aspects of a length frequency distribution were calculated for each stream sample. Size frequency distribution qualities examined included central tendency, spread, shape, diversity, and distance, where diversity measures were calculated treating length categories as species, and distance measures were Euclidean distances between size frequencies distributions per stream and cumulative size frequencies across and within subdrainages in the North Fork. Environmental variables examined were cutthroat trout density (CUTDEN), stream drainage area (AREA), Strahler stream order of the receiving stream (RORDER), and basin identity (BASIN). Two nuisance variables, year of sampling (YEAR) and sample size (N) had significant effects on size structure in many of the regression models explored. None of the four environmental variables had clear and consistent effects on size structure metrics, but some patterns emerged. RORDER had weak relationships to distance and diversity metrics, and had no effects on central tendency, spread, or shape metrics. AREA had weak but fairly consistent effects on some spread and diversity metrics. BASIN demonstrated weak effects on mean, some diversity metrics, and one Euclidean distance metric. CUTDEN appeared to affect measures of central tendency and spread but not shape, diversity, nor distance metrics. Size structure metrics may be able to be selected that maximize sensitivity to variables of interest while minimizing sensitivity to nuisance variables and study design limitations. Use of a suite of size metrics provided more information regarding westslope cutthroat trout size structure relationships with environmental variables than would have been gained by focusing only on mean or maximum length, size metrics most commonly reported in the literature. Size structure analyses including multiple metrics may provide valuable information regarding the spatial distribution of intraspecific phenotypic diversity and its responsiveness to environmental variables.

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INTRODUCTION

Phenotypic diversity includes the intraspecific variation within and between populations in traits such as morphology and behavior, and plays a critical part in many evolutionarily and ecologically essential functions including the ability to adapt to local conditions and disturbance regimes, population differentiation that leads to speciation, and the ability to reduce intra- and interspecific competition through niche differentiation. Fish exhibit greater intraspecific phenotypic variation than other taxa (Allendorf et al. 1997). Although each species can be characterized with regard to life history traits, considerable variation within and between populations is characteristic of most Pacific salmonids (Healey 1986 as cited in Gresswell et al. 1994). Recognition and consideration of this variability is critical for successful conservation of fish biodiversity at the species level (Gresswell et al. 1994). Considerable effort has been expended toward understanding genetic and life history variation in Pacific salmon, allowing for characterization and discrimination of discrete stocks (e.g. Miller and Brannon 1981; Healey 1986 as cited in Gresswell et al. 1994; Halupka et al. unpublished manuscript). Considerably less effort has been directed toward understanding genetic and life history variation in inland trouts and chars (Gresswell et al. 1994). Yet many of the same conditions and mechanisms responsible for producing species substructuring have been documented in inland salmonids, including homing to natal streams, genetic variation among populations, and residence in diverse and distal habitats.

Although fish exhibit higher intraspecific phenotypic diversity than most taxa, they do not express concomitant higher levels of genotypic variation. Allendorf (1988) draws two conclusions: 1) focus on only genetic diversity will fail to conserve a significant component of intraspecific fish diversity, and 2) fish are more susceptible to environmental factors than are other taxa. Phenotypic characterization of a species is critical to many conservation questions, including understanding of population structure, identification of taxonomic units to conserve, relationships between phenotypic variation and habitat complexity, scales at which phenotypic variation is expressed, and details of refuge design. Angermeier and Schlosser (1995) emphasize that the ecological and evolutionary contexts of each biodiversity component must also be considered. Conservation of not only existing biodiversity, but also processes such as gene flow and local adaptation to diverse habitats that generate biodiversity are critical (Erwin 1991). Although phenotypic diversity such as life history and morphological differences have been used historically in conjunction with genetic information to differentiate between stocks of commercial fish species, its usefulness for addressing conservation questions is relatively unexplored.

Organism size has been recognized as an important scaling variable for comparison of various biological processes, including metabolism, growth, production rates, reproductive condition and commitments, and constraints on body form and function (Policansky 1983; Stein et al. 1987), and a considerable body of literature exists on the subject (e.g. Peters 1983; Schmidt-Neilsen 1984; Werner and Gilliam 1984). Body size is one of an organism's most important attributes from both ecological and evolutionary perspectives. For example, Foote (1988) found male mate choice to be dependent on male size in salmon; larger males were able to select larger females and thereby increase their fitness since larger females tend to be more fecund and have access to better redd sites. Body size helps to explain organism distribution across habitats (Crowl et al. unpublished manuscript; Larscheid and Hubert 1992), and body size is a significant factor mediating ontogenetic niche shifts (Werner and Gilliam 1984; Stein et al. 1987). Interspecific and intraspecific competition and predation relationships can change dramatically as an organism grows and its role in a community changes with size. In understanding mechanisms of community structure and function, organisms must therefore be organized by both species and size, particularly in taxa with high size variability within age groups, such as fishes (Werner and Gilliam 1984). Examination of community structure based on size distribution while ignoring species identities may be appropriate in some systems since many species' functional roles within a community change with size (Stein et al. 1987; Reimchen

1990). Body size can be used as an organizing principle, just as are species diversity, productivity, trophic structure, and functional processes.

Environmental variation in size structure has been documented in salmonids; however, little effort has been directed toward linking population size structure with specific environmental gradients. Body size is strongly influenced by environmental factors such as temperature, food availability, and presence of competitors (Smoker et al. 1994). Crowl et al. (unpublished manuscript) found a direct relationship between Colorado River cutthroat trout size (*Oncorhynchus clarki pleuriticus*) structure diversity and habitat complexity. Different size categories of fish were associated with different habitat variables, suggesting that complex habitat supports greater population size structure diversity. Johnson et al. (1992) found size structure of brook trout in Wyoming ponds to be positively correlated with habitat variables such as depth, surface area, volume, and late-summer water temperature and negatively correlated with extent of water-level fluctuation and a measure of recruitment potential. They focused on mean total length, mean weight, relative weight, and proportional stock density. Larscheid and Hubert (1992) found large brook trout to be associated with location in the watershed and channel gradient as well as salmonid community composition. Large brook trout were associated with stream reaches lower in the watershed and of lower gradient, conditions that may result in greater productivity and therefore growth potential. Lukens (1978) found a similar relationship with westslope cutthroat trout; larger individuals tended to be located in larger streams and smaller fish in smaller streams. Female size in coho salmon was correlated with deeper redds, which in turn were found to be less vulnerable to flooding and competition from other redd-building females (van den Berghe and Gross 1984). McDonald and Hershey (1989) found size structure of a lake trout population to be influenced by angling. They sampled in 1977 (prior to) and 1986 (post) angler exploitation and found median size to be significantly reduced in 1986, and below the 1977 reproductive size.

Although relationships between mean size, growth, and growth rate and environmental variables affecting growth opportunity such as food availability, competition, system productivity, and temperature have been relatively well studied, most empirical work has focused on mean size (e.g. Lukens 1978, Johnson et al. 1992, Larscheid and Hubert 1992 as discussed above). Variation in size has generally been treated as a nuisance, rather than an important source of information regarding population structure. Other components of population size structure, such as the relative proportions of large fish, juvenile fish, the numbers of sizes represented in the population, and the range of sizes represented, are relatively unexplored components of a

population's size structure. In species-depauperate communities, niche width may be wider than in species-rich communities, with each species potentially filling multiple niches (Crowl et al. unpublished manuscript). In simple salmonid communities, distribution of individuals across available niches may be size-based since other processes such as ontogenetic niche shifts and competitive and predator-prey relationships are size driven. Species diversity indices applied to fish size classes may provide valuable information concerning population size structure and relationships with habitat gradients.

Aquatic processes and relationships are fairly well understood at watershed and smaller scales (e.g. Frissell et al. 1986; Montgomery et al. 1995; Imhof et al. 1996; Poole et al. 1997). However, important processes and resources such as migration and distribution of spawning areas and winter refuges occur at larger spatial scales. Dynamics and habitat relationships are not well understood at these larger scales. In addition, many trout and salmon species are in decline in the Pacific northwest, and recovery efforts must include large spatial scales to conserve intraspecific genetic and phenotypic diversity (Allendorf 1988; Franklin 1993) and the habitat templates to which diversity-generating processes respond (Healey and Prince 1995). The objectives of this study were to 1) examine relationships between population size structure of westslope cutthroat trout (*Oncorhynchus clarki lewisi*) and environmental variables such as stream position within a subbasin and between drainages, trout density, and drainage area, and 2) explore relative performance of size structure metrics, through analysis of an existing 3-year size structure dataset from the North Fork Coeur d' Alene subbasin, northern Idaho.

METHODS

Dataset The dataset used in all analyses was obtained from the Rocky Mountain Research Station, U.S. Forest Service, Boise, Idaho. Fish collections were made in 1994, 1995, and 1996 in many streams in the Little North Fork and North Fork drainages of the Coeur d' Alene River, northern Idaho. This subbasin comprises approximately 2280 km² and elevation ranges from 700 to 1850 m above sea level (Dunnigan 1997). Historically, 2nd- and 3rd-order tributaries such as were sampled in this dataset contained westslope cutthroat trout, bull trout (*Salvelinus confluentus*), and several sculpin species; however, bull trout has been extirpated from this subbasin and rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*) have been introduced. Methods of fish collection are described more fully by Dunnigan (1997). For each stream, total stream length on a 7.5 minute quadrangle USGS topographic map was

divided into three equal-length reaches, and 3, 30-m long sites were randomly selected and sampled within each reach. Eight of the 9 sites were sampled by single-pass electrofishing and the ninth was randomly selected and sampled by triple-pass electrofishing. All trout collected were identified and measured. Samples were collected by different people within years and between years, following standardized procedures. These data were originally collected to examine relationships between fish abundance and habitat characteristics. Because length frequency distributions are sensitive to sample size, samples sizes less than 40 westslope cutthroat trout per stream were excluded from analyses. Insufficient samples would have been available to conduct analyses if restricted to larger sample sizes. Sample size and year of collection were treated as nuisance variables, and relationships with size structure metrics were examined. Of the 176 samples taken from 84 streams, 74 samples from 53 streams had sample sizes sufficient for inclusion in analyses. Of these, only 69 samples were useful in most analyses due to missing data for one or more independent variables.

Size Structure Metrics Size structure metrics were selected to represent a variety of qualitative aspects of a size frequency distribution. Metrics represented central tendency, spread width, curve shape, diversity, and Euclidean distance from cumulative size frequency curves (Table 1). Standard descriptive statistics, including mean, median, range, variance, skewness, kurtosis, 50% confidence interval width, and number of modes were calculated for each collection using Systat (Systat Version 8.0, SPSS, Inc. 1998, Standard Version). The middle 75% confidence interval width was calculated by subtracting the lower 75% confidence interval limit from the upper 75% confidence limit. Number of modes was counted visually from Systat density function kernel curve plots. For each sample, fish were placed in size categories to examine usefulness of species diversity indices. The effect of size category (bin) width was explored by placing individuals in two bin widths, 10mm and 20mm. Number of bins occupied and d (species richness) were then calculated for each bin width, treating bins as species. Simpson (D) and Shannon (H') indices were calculated for only 10mm bin width data. Euclidean distances based on size frequencies were calculated for the 10mm bin width between samples and total cumulative subbasin frequencies (EUQFQ1) and cumulative frequencies within their respective drainages (Little North Fork versus North Fork; EUQFQ23). Formulas and references for indices used in analyses are given in Table 2.

Environmental Variables Three variables were examined that described spatial aspects of study streams. RORDER, the stream order of the receiving stream to which study streams drained, was taken from 7.5 minute quadrangle USGS topographic maps using Strahler stream orders. AREA, the area of each study stream above its confluence with the receiving stream, was produced by ArcInfo and provided by U.S. Forest Service personnel. BASIN was used to differentiate streams in the Little North Fork drainage from streams in the North Fork Coeur d'Alene drainage. Cutthroat trout density (CUTDEN), calculated as the average density from fish count and habitat area information provided in the dataset, was also examined as an environmental variable. These variables were selected since each would be predicted to have effects on at least some aspects of fish size. For example, CUTDEN may affect the ability of territorial species like salmonids to acquire and defend sufficient food and space resources for growth and survival. As CUTDEN increases, mean fish size may be expected to decrease or the number of sizes of fish able to survive may decrease. BASIN may be an effective predictor of fish size since land use history and current instream conditions in the Little North Fork and North Fork drainages are somewhat different (Dunnigan 1997). Stream size, which can be quantified as the area draining to a point, has been shown to be positively correlated with fish size (e.g. Lukens 1978; Larsheid and Hubert 1992), and may also affect size variance. Size of the receiving stream (RORDER) may also affect fish size structure since small fish in small streams may perceive the receiving stream, if large and therefore containing significantly different habitat conditions, to function as a barrier to movement. Streams draining to large RORDER streams may therefore be expected to have lower size spread if fish in neighboring tributaries are isolated from each other.

Analyses All variables were examined for normality within year of collection, including skewness, kurtosis, homogeneity of variance, and independence of mean and variance. Skewness and kurtosis were calculated by Systat. Box and whisker plots and normal probability plots were examined visually. With few exceptions, all variables were found to be normal for all years. Since sample size (N=74) is fairly large, variables should be relatively robust to minor deviations from normality. However, MODES in particular is unlikely to be normal since most samples have MODES equal to 2 or 3. Since stream selection may not have been conducted randomly, both regression and correlation analyses were conducted. For all independent variables, multivariate and univariate regression models were conducted to identify variables

significantly affecting size structure metrics. Size structure metrics more sensitive to each independent variable were identified in univariate analyses and by examining canonical correlates in significant multivariate analyses. All univariate and multivariate linear regression analyses were conducted using SAS (SAS Institute, Inc., Release 6.12 TS060, Copyright 1989-96). Linear correlations were examined to provide additional information regarding relationships between independent variables and size structure metrics. Correlations were calculated by Systat. In the original data collection, several streams were sampled twice during 1994 to examine abundance consistency within year. Only four streams were sampled twice and had samples of 40 or more fish during each sampling period. These few samples were used to examine temporal changes in size structure across the sampling period during 1994. Wilcoxon signed-rank tests were conducted to examine differences in size structure metrics between sampling periods. Additional variables such as sample size (N) and year of collection (YEAR) were included in analyses to examine the effects of these "nuisance" variables on size structure metrics.

RESULTS

Multivariate and univariate regression models were examined for variables of interest (environmental and nuisance variables) singly and in various combinations to explore relationships between size structure variables and independent variables and to identify size structure metrics having the greatest effect on size structure. Sample size was insufficient to allow examination of models containing more than three or four independent variables. Therefore, regression models were examined with single variables, with both nuisance variables (N, YEAR), with significant nuisance variables combined with environmental variables of interest (AREA, RORDER, BASIN, CUTDEN), and with only environmental variables of interest in various combinations. Wilks' Lambda was used as the test statistic for all multivariate analyses. Summaries of model results are presented in Table 3 (N, YEAR) and Table 4 (environmental variables).

Nuisance Variables

Sample Size In a multivariate regression analysis with N as the only independent variable, the model was highly significant ($p < 0.0001$; Table 3). Metrics for which N was significant in

univariate analyses included MEAN, MEDIAN, MID75, MODES, BINS10, BINS20, D20, EUQFQ1, and EUQFQ23. Multivariate models with N, YEAR, and BASIN or CUTDEN revealed similar strong relationships between N and size structure metrics. Canonical correlates in the multivariate model with only N indicated that MEAN, MID75, and SWH10 were the most important size metrics. Models with YEAR and either CUTDEN or BASIN were less conclusive in suggesting important size metrics. With CUTDEN, MEAN and MID75 were suggested, and with BASIN, MID75, EUQFQ23, and EUQFQ1 were suggested. However, in these latter two models, within canonical structure and standardized canonical coefficients agreed to only a limited degree. A models with N, YEAR, and RORDER was not significant for N. A model with N and AREA + YEAR was significant for N ($p < 0.01$). Several size structure metrics were strongly correlated with N, including MID75 ($r = -0.647$) and BINS10 ($r = 0.468$). Most analyses agreed that sample size significantly affected some size structure metrics, most consistently MEAN, MID75, and several of the diversity metrics.

Year In general, YEAR was not a significant component of multivariate models (Table 3). Alone or with N and CUTDEN, RORDER, or AREA, YEAR was not significant. Only with N and BASIN did YEAR play a significant role in the model. In univariate analyses, YEAR affected diversity and distance metrics such as D20, SIMPD10, SWH10, EUQFQ1, and EUQFQ23 in some but not all models. In the multivariate model with N and BASIN, standardized canonical coefficients and within canonical structure both suggested that BINS20 and D20 were relatively strong size metrics. Both also indicated some importance of MEAN and MID75, but disagreed on their strength relative to other metrics. YEAR generally did not affect central tendency, spread, or shape variables, with the exception of weak indication by canonical correlates of the importance of MEAN and MID75 in one multivariate model examined. No size metrics were strongly correlated with YEAR (all $r < 0.24$).

Time of Sampling (within year) In Wilcoxon signed rank tests ($N=4$), no size structure metrics were significantly different between sampling times. CUTDEN ($N=3$) and N were also not significantly different between sampling times. However, several variables did demonstrate consistent trends ($p=0.068$): VAR, RANGE, MID75, and KURT were lower during the first sampling period than the second for all samples, and EUQFQ23 was greater during the first sampling period for all samples.

Environmental Variables

Area In multivariate models by itself and with N + YEAR and with N + CUTDEN + RORDER, AREA did not significantly affect size structure. AREA was a significant component of multivariate models by itself ($p < 0.05$), with BASIN + RORDER ($p < 0.05$), and with N + YEAR + BASIN ($p < 0.001$; Table 4). In multivariate models for which AREA was significant (BASIN + RORDER, and N + YEAR + BASIN), interaction components were also significant. No central tendency, shape, or distance variables appear to be affected by AREA; RANGE, VAR, MID75, BINS10, and BINS20 were consistently significant in univariate models. For the three multivariate models in which AREA was significant, no size metrics were consistently most important as indicated by canonical correlations. With AREA as the only independent variable, RANGE, VAR, and BINS10 were significant metrics, consistent with univariate analyses. However, with BASIN + RORDER, KURT and EUQFQ23 were the most significant metrics, and with N + YEAR + BASIN, D10, D20, and EUQFQ23 were the most significant metrics. No size structure variables had strong correlations with AREA (largest $r = 0.429$ for RANGE).

Receiving Stream Order RORDER was not a significant component of most multivariate models explored. Exceptions include a model with no other independent variables, and a model with N + BASIN. In univariate analyses, SIMPD10, EUQFQ1, and EUQFQ23 were consistently affected by RORDER. Other metrics affected but less consistently so include BINS10, D10, and SWH10. No central tendency, spread, or shape variables appear to be affected by RORDER. Only two multivariate models examined suggested significant effect of RORDER on size structure metrics, and in neither of these models did examination of canonical correlations suggest strong involvement by any particular size structure metrics. No size structure variables have strong correlations with RORDER (largest $r = -0.308$ for EUQFQ1).

Basin Although results presented in Table 4 suggest that BASIN may be a significant factor for some size structure metrics since BASIN was a significant variable in most multivariate models explored, BASIN was not independent of N or YEAR (see Table 3). Multivariate models explored that did not contain these variables did not indicate any significant effects of BASIN on size structure metrics. In addition, most models contained significant interaction terms for all combinations. In univariate models, BINS10, BINS20, and SWH10 were consistently affected by BASIN; however, effects may be due to interaction effects with N and/or YEAR. No central

tendency or spread variables appear affected by BASIN. KURT was significantly affected by BASIN in a univariate model with RORDER and CUTDEN. Examination of canonical correlations in multivariate analyses for which BASIN was a significant factor suggest that MEAN, EUQFQ1, and possibly BINS10, BINS20, and D20 were affected by BASIN. These results are relatively inconsistent with univariate results. Diversity and distance metrics tended to be more strongly correlated with BASIN; however, no size structure variables are strongly correlated with BASIN (largest $r = 0.342$ for D20).

Cutthroat Trout Density CUTDEN was generally not a significant component of multivariate models explored (Table 4). It was significant in a regression model with no other independent variables and in a model with N + AREA. It appears to strongly affect some measures of central tendency (MEAN, MEDIAN), spread (MID75), and diversity (BINS10, BINS20, D20) in univariate analyses. SIMPD10 and SWH10 were significantly affected in one model (N + YEAR) and SKEW and EUQFQ1 were each affected in one model (BASIN + RORDER, and N + RORDER, respectively). Multivariate models in which CUTDEN was significant suggest that MEAN and MID75 may be the most important size structure metrics. This is somewhat consistent with univariate model results and correlation analyses (below). Importance of EUQFQ23 and D20 was also indicated by one model. Several size structure metrics have strong correlations with CUTDEN, including MEAN ($r = -0.464$) and MID75 ($r = -0.663$). Diversity and density metrics appear relatively independent of CUTDEN, with consistently low correlation coefficients.

Size Structure Metric Comparisons

Many multivariate analyses for which an independent variable significantly affected size structure metrics suffered from significant interaction terms, weak relationships between independent and dependent variables, and inconsistencies between standardized canonical coefficients and within canonical structure. Some size metrics were highly correlated, within and between qualitative characteristics, whereas others were highly differentiated. Correlation results are discussed below and presented in Tables 5a (spread metrics), 5b (shape metrics), 5c (diversity metrics), and 5d (across qualitative categories). Across qualitative categories, some strong correlations were evidenced. Variables expected to be correlated include MEAN and SKEW ($r = -0.50$), MEAN and SIMPD10 ($r = -0.50$), and RANGE and BINS10 ($r = 0.74$). Other correlations that were not expected include BINS10 and EUQFQ1 ($r = -0.52$) and SIMPD10 and EUQFQ1 ($r = 0.77$). It is not obvious why these latter pairs should be correlated.

Central Tendency The correlation coefficient between MEAN and MEDIAN was $r = 0.90$.

Therefore, it would be expected that these metrics should respond similarly to independent variables. Measures of central tendency (MEAN, MEDIAN) were significantly affected primarily by N and CUTDEN, both of which produced significant effects on both size metrics in a variety of univariate models. Examination of canonical correlations indicates that MEAN is affected by N in most multivariate models examined, and may be affected in some models by BASIN and CUTDEN, and possibly YEAR. CUTDEN showed the strongest correlations with both MEAN and MEDIAN ($r = -0.464$ and -0.378 , respectively). Correlations between MEAN and MEDIAN and N were $r = -0.345$ and -0.287 .

Spread Correlation coefficients (r) for spread variables are presented in Table 5b. VAR is moderately correlated with MID75 and RANGE (0.7 and 0.8 respectively). Of the 6 independent variables examined, VAR was affected only by AREA, and in only one model, in univariate analyses (Table 4). None of the metrics of spread were affected by YEAR, BASIN, or ORDER. AREA appears to have some effect on spread metrics, particularly RANGE but also VAR reported above and MID75 in some models. MID75 also appeared to be affected by N and CUTDEN. RANGE was affected by CUTDEN in one model. Examination of canonical correlations indicated that MID75 was weakly affected by YEAR and CUTDEN, and RANGE and VAR may be affected by AREA. CUTDEN and N were relatively strongly correlated with MID75 ($r = -0.668$ and -0.659 , respectively). No other size metrics were strongly correlated with any independent variables.

Shape Correlation coefficients (r) between shape metrics are presented in Table 5b. KURT and SKEW are moderately correlated ($r = 0.70$); as expected other correlations are relatively weak since each metric represents a different characteristic of a length frequency distribution. Shape variables generally were little affected by any independent variables in any univariate models. SKEW was significantly affected by CUTDEN in one model, KURT was significantly affected by BASIN in one model, and MODES was significantly affected by N in most models. Examination of canonical correlates in multivariate analyses indicated a significant role for no shape variables in any models examined for any variables. No strong correlations were found between any shape variables and any independent variables (largest $r = 0.32$ between MODES and N).

Diversity Correlation coefficients (r) between metrics of diversity are presented in Table 5c. BIN metrics are relatively strongly correlated with each other and with SIMPD10 and SWH10, whereas they are relatively weakly correlated with D10 and D20. D10 and D20 are relatively strongly correlated with each other, as are SIMPD10 and SWH10. D10 and D20 differ from the other metrics since they adjust for sample size differences. Diversity metrics appear to be more sensitive to all of the independent variables examined than are central tendency, spread, or shape variables. All six independent variables strongly affected one or more diversity metrics in univariate models. N consistently affected BINS10 in all univariate models examined and BINS20, D20, and SWH10 in most models. However, canonical correlates in multivariate analyses failed to identify diversity metrics as being particularly sensitive to sample size; MEAN and MID75 and distance measures were most consistently identified as sensitive to N in these analyses. SWH10 was a moderately important metric in a multivariate model with only N, however. YEAR affected SIMPD10 in two models and BINS10, BINS20, D20, and SWH10 in at least one model. AREA affected BINS10 and BINS20 in most models and D20 in one model, but not other diversity metrics. RORDER affected SIMPD10 in all but two models, SWH10 in several models, and D10 and BINS10 each in one model. BASIN fairly consistently affected BINS10, BINS20, and SWH10, and also affected D10 in one model. CUTDEN most strongly affected BINS10 and BINS20, but also affected D20, SIMPD10, and SWH10 in one or more model. Examination of canonical correlates from multivariate analyses supports the sensitivity of BINS20 and D10 to BASIN, and also suggests that D20 may be sensitive to this variable. RANGE, VAR, BINS10, D10, and D20 were indicated as important size metrics sensitive to AREA in one or more models, consistent with univariate analyses. D20 was the only metric sensitive to CUTDEN in multivariate canonical analyses. No size metrics were particularly responsive to RORDER in multivariate analyses. Correlation coefficients between independent variables and most diversity metrics were relatively low. The highest r value was between N and BINS10 ($r = 0.464$). All other relationships had r values lower than 0.40.

The effect of length interval (bin) width was explored through comparison of regression model results between two size structure variables calculated for bin widths of 10mm and 20mm (BINS10 versus BINS20 and D10 versus D20) and correlation analysis. Correlation coefficients between BINS10 and BINS20 and D10 and D20 were 0.88 and 0.87, respectively. In univariate regression analyses, BINS10 and BINS20 performed similarly in most cases. Both were significantly affected by N in most models and BASIN and CUTDEN in some models. BINS10 appears slightly more sensitive to variables such as YEAR and RORDER, with significant

relationships in some models, whereas BINS20 demonstrates little relationship to these variables. Conversely, D20 appears slightly more sensitive to independent variables than does D10. D20 is significantly affected by N in 3 of 5 univariate models examined, whereas D10 shows no significant relationship to N. D20 is also more sensitive to YEAR and AREA. CUTDEN significantly affected D20 in some but not all models. BASIN appeared to significantly affect D10 but not D20 in one model, however. Neither were affected by RORDER. In significant multivariate models, none of the four variables consistently had a strong role. In other significant models, diversity variables were not particularly strong relative to other variables.

Distance The correlation coefficient for EUQFQ1 and EUQFQ23 is $r = 0.95$. Therefore, it would be expected that these variables would be similarly affected by independent variables. EUQFQ1 and EUQFQ23 showed consistent sensitivity to N, RORDER, and YEAR, and no sensitivity to AREA or BASIN in univariate analyses. EUQFQ1 was significantly affected by N in all 5 univariate models examined, and EUQFQ23 was significantly affected in 4 out of 5 models. Two models with significant YEAR effects also included effects on both distance metrics, and 4 out of 5 models with RORDER included one of the distance variables. CUTDEN appears to have little effect on distance metrics in univariate analyses; only one model contained one of these metrics, EUQFQ1. Canonical analyses in multivariate models are somewhat inconsistent with univariate results. Only one of three models with N indicated importance of distance metrics; both EUQFQ1 and EUQFQ23 were indicated as moderately important metrics in this model. Neither of the two distance metrics were indicated as important metrics in the one multivariate model for which YEAR was significant. Two multivariate models with BASIN suggested that both EUQFQ1 and EUQFQ23 were important size metrics. No RORDER models indicated any significant role for distance metrics. EUQFQ23 was an important metric in one of 4 models with CUTDEN and two of 3 models with AREA. No correlation coefficients between distance metrics and independent variables were strong; the largest r was between N and EUQFQ1 ($r = -0.294$).

DISCUSSION

Use of data collected for other than the desired purpose can lead to numerous challenges in analysis and interpretation of results. Several methodological limitations restricted

analyses in this paper. However, location of datasets containing desired information and representing a relatively large spatial extent are few. The Coeur d' Alene dataset used in this analysis is rare in its spatial scope in particular but also in containing data from multiple years. Because the data were collected to examine westslope cutthroat trout abundance, sufficient samples sizes were often not obtained for adequate length frequency analyses. Unfortunately, information from many of the sampled streams could not be used. A larger number of streams would have allowed for more thorough examination of regression models by allowing inclusion of all variables of interest. Patterns may also have been clearer with larger samples and additional sampled streams. Although within-year effects were explored in this paper, sample size ($N=4$) was inadequate for meaningful analyses. Another approach for examining within-year effects that could be pursued using the same dataset would be to compare all sites collected early in the sampling period from those collected late in the sampling period (sampling period was approximately July 15 – September 1 of each year).

Interactions between variables were identified in several instances. Some were expected and are a product of collection methods. For example, cutthroat density (CUTDEN) and sample size (N) were closely correlated ($r = 0.82$), since all fish were collected in a defined total length of stream. Better methods to examine size structure would have been to sample for a minimum number of fish regardless of stream length, reducing the correlation between CUTDEN and N . The difference between the D and $BINS$ variables was sample size since d is a richness measure that controls for minor differences in sample size. Larger differences in N were controlled for by restricting analyses to sample sizes greater than 40. In general, $BINS$ variables were more sensitive to sample size than were D variables as expected, although $D20$ was significantly affected by N in some models. D variables may be more useful than $BINS$ in further analyses of size structure. A relationship between the $EUQFQ$ variables and $BASIN$ was expected but not found. $EUQFQ1$ quantifies the Euclidean distance between length frequency distributions of each individual stream and the cumulative length frequency distribution of the entire sampling area, whereas $EUQFQ23$ uses cumulative length frequencies of each drainage (Little North Fork versus North Fork). It therefore might be expected that $EUQFQ1$ would be more sensitive to $BASIN$ than $EUQFQ23$ since basin identity is accounted for in $EUQFQ23$ but not $EUQFQ1$. No such pattern was identified. Other interactions between variables were evidenced, and may be a product of the overall significance of variables such as sample size. Study designs minimizing ability of variables to interact and further characterizing interactions

would be desirable in future work exploring relationships between environmental variables and size structure metrics.

Both “nuisance” variables (N, YEAR) affected size metrics to some degree. Sample size appears to be a significant factor affecting the relationships between many size structure metrics and environmental variables of interest. Diversity metrics in particular are expected to be sensitive to sample size since dependency of species richness on sample size is a well-documented problem in quantifying species diversity and comparing diversity among sites (Krebs 1989). Additional effort should be expended toward determining at what sample size dependency of diversity metrics in particular and other metrics as well begin to decline or disappear. Inclusion of samples as small as 40-70 may have made identification of important patterns difficult in these analyses, but insufficient numbers of streams would have been available if analyses had been restricted to samples with more than 70 individuals. Year of sampling appeared to affect only distance and diversity metrics, and only in some models. Size metrics integrating multiple aspects of a size frequency distribution (diversity, distance) may be more sensitive to environmental gradients, but may also be more sensitive to study design features and nuisance variables than are metrics quantifying only one aspect of a size frequency distribution.

Environmental variables examined have relatively weak and unclear relationships to size structure metrics, although some patterns emerged. Receiving stream order (RORDER) had some effect on distance and diversity measures, but no effect on measures of central tendency, spread, or shape. Relationships of these variables to spread metrics were predicted but not seen. AREA appeared to weakly affect spread variables and some diversity metrics. Relationships between area and variation in many biological and environmental phenomena might be expected, since as area increases, the diversity of habitat conditions contained within increases. Ability to detect differences in size due to AREA in this analysis may have been limited in this analysis since all streams selected for sampling were 2nd or 3rd order, and therefore a limited range of drainage areas were included. Dunnigan (1997) found a relationship between presence of young-of-the-year westslope cutthroat trout and drainage area and stream order when a larger range of stream sizes were examined. Basin identity (BASIN) had weak effects on MEAN, some diversity measures, and EUQFQ1 in some models, but results were inconclusive. Relationships between cutthroat trout density (CUTDEN) and size structure metrics were not strong, but CUTDEN appears to have some effect on measures of central tendency and spread and no effect on measures of diversity or distance. Therefore, in spite of

limitations in interpretation of results, and inconsistencies between types of analyses, size structure metrics within and between qualitative categories appear to be differentially sensitive to environmental variables. Univariate analyses provide the most information regarding relationships between environmental variables and size structure metrics, but likely fail to reveal dependent and independent variable interactions. A suite of size structure metrics may be able to be identified that are maximally sensitive to a particular environmental variable of interest while minimizing responsiveness to nuisance variables and limitations in study design.

Metrics included in this study behaved differently, collectively providing a suite of measures quantifying different aspects of a length frequency distribution. Some variables were strongly correlated, particularly within a size frequency quality (e.g. MEAN versus MEDIAN). Additional multivariate analyses may help to provide additional understanding of relationships between size structure metrics and to help identify metrics that are highly redundant. Some metrics are highly sensitive to sample size, and should either be restricted from multivariate models or sampling methodologies should be modified in future studies to reduce the influence of N on size structure metrics, whereas some metrics are much less responsive to N (e.g. D10). “Nuisance” variables significantly hindered analysis and understanding of relationships between size structure metrics and variables of interest in this analysis.

Most studies examining size structure focus on mean length, maximum length, and/or some minimum length applicable to harvest desirability, and may also include weight measures. Inclusion of only those metrics in this analysis would have missed important information regarding relationships between size structure of westslope cutthroat trout populations and environmental variables. Several size structure metrics explored in this study and not examined elsewhere in the literature were relatively sensitive to independent variables examined in this analysis. In particular, diversity and distance measures have not been examined prior to this analysis and were responsive to environmental variables. Diversity measures were sensitive to most variables examined. Distance measures demonstrated moderate sensitivity to N and RORDER and limited sensitivity to BASIN, CUTDEN, AREA, and YEAR. Size structure analyses including multiple metrics may provide valuable information regarding the spatial distribution of intraspecific phenotypic diversity and its responsiveness to environmental variables.

Results from this analysis offer direction for further examination of relationships between fish size structure and the ecological context in which fish populations grow. Further exploration of the relative performance of size structure metrics, as well as development of the ecological

basis in theory, will be necessary before size structure relationships and useful analytical methods can be identified. A relationship between watershed area and size structure variation is suggested by this analysis, as might be expected. Additional exploration using datasets collected for the purpose may confirm a relationship and provide additional information as to its nature, as well as clarify why distance metrics did not evidence the same relationship. Additional exploration of the relationship between cutthroat density and size metrics may also prove fruitful. Density effects might be expected as functions of competition and predation (cannibalism). Study design will have to consider the multiple roles of density as an indirect effect of other environmental variables as well as a direct modifier of size structure.

Table 1. Size structure metrics used in all analyses.

Size Structure Quality	Description of Metrics	Variables
Central tendency	Mean, median	MEAN, MEDIAN
Spread	Range, variance, width of 75% confidence interval	RANGE, VAR, MID75
Shape	Skewness, kurtosis, number of modes	SKEW, KURT, MODES
Diversity	Number of bins (width = 10mm, 20mm), d, H', D	BINS10, BINS20, D10, D20, SWH10, SIMPD10
Distance	Euclidean distance from cumulative size frequency distribution	EUQFQ1, EUQFQ23

Table 2. Formulas and descriptions for calculated variables used in analyses.

Variable	Description
BINS10	# bins occupied, where bin width = 10mm
BINS20	# bins occupied, where bin width = 20mm
D10	$BINS10/\log N$ = species richness, corrected for differences in sample size
D20	$BINS20/\log N$ = species richness, corrected for differences in sample size
SIMPD10	Simpson Index, $D = 1/C$ (Meffe and Carroll 1994)
SWH10	Shannon Index of equitability, H' (Krebs 1989)
EUQFQ1	Euclidean distance between site and total cumulative size frequencies (bin width = 10mm; Krebs 1989)
EUQFQ23	Euclidean distance between site and basin cumulative size frequencies (bin width = 10mm; Krebs 1989)

Table 3. Summary of regression analyses for variables N and YEAR.

Variable	Covariates in Model	Multivariate		Univariate
		Significance of Variable ¹	Interaction Variables Significant ²	Size Metrics Significant for Variable ³
N	None	p<0.0001	-----	MEAN, (p<0.01), MEDIAN (p<0.01), MID75 (p<0.0001), MODES (p<0.01), BINS10 (p<0.0001), BINS20 (p<0.01), D20 (p<0.05), SWH10 (p<0.01), EUQFQ1 (p<0.01), EUQFQ23 (p<0.05)
N	YEAR, BASIN	p<0.0001	ALL (p<0.0001)	MID75 (p<0.0001), MODES (p<0.002), BINS10 (p<0.0002), BINS20 (p<0.02), D20 (p<0.03), SWH10 (p<0.03), EUQFQ1 (p<0.02), EUQFQ23 (p<0.01)
N	YEAR, CUTDEN	p<0.01	CUTDEN (p<0.05), YEAR (p<0.01), CUTDEN*YEAR (p<0.05)	MEAN (p<0.05), MEDIAN (p<0.05), MID75 (p<0.0001), BINS10 (p<0.0001) ⁴ , BINS20 (p<0.01), D20 (p<0.05), SWH10 (p<0.01) ⁴ , EUQFQ1 (p<0.01) ⁴ , EUQFQ23 (p<0.05) ⁴
N	YEAR, RORDER	NS	-----	MID75 (p<0.0001), MODES (p<0.01) ⁴ , BINS10 (p<0.0001), BINS20 (p<0.01) ⁴ , SWH10 (p<0.01), EUQFQ1 (p<0.01), EUQFQ23 (p<0.05)
N	YEAR, AREA	p<0.01	None	MEAN (p<0.01), MID75 (p<0.0001), RANGE (p<0.05) ⁴ , BINS10 (p<0.0001) ⁴ , BINS20 (p<0.01), SWH10 (p<0.01) ⁴ , EUQFQ1 (p<0.01) ⁴ , EUQFQ23 (p<0.05) ⁴
YEAR	None	NS	-----	D20 (p<0.05), SIMPD10 (p<0.01), SWH10 (p<0.03), EUQFQ1 (p<0.001), EUQFQ23 (p<0.002)
YEAR	N, BASIN	p<0.001	ALL (p<0.0001)	BINS10 (p<0.05), BINS20 (p<0.05), D20 (p<0.05), SIMPD10 (p<0.01), SWH10 (p<0.01), EUQFQ1 (p<0.01), EUQFQ23 (p<0.01)
YEAR	N, CUTDEN	NS	-----	SIMPD10 (p<0.05)
YEAR	N, RORDER	NS	-----	None
YEAR	N, AREA	NS	-----	SIMPD10 (p<0.05) ⁴ , SWH10 (p<0.05) ⁴ , EUQFQ1 (p<0.01) ⁴ , EUQFQ23 (p<0.01) ⁴

¹ NS = Not significant² only if multivariate model was significant for variable³ only if overall univariate model was significant; significant models where only interaction terms were significant are not reported⁴ interaction terms also significant

Table 4. Summary of regression analyses for environmental variables AREA, RECORDER, BASIN, CUTDEN.

Variable	Covariates in Model	Multivariate		Univariate
		Significance of Variable ¹	Interaction Variables Significant ²	Size Metrics Univariate Significant for Variable ³
AREA	None	p<0.05	-----	RANGE (p<0.001), VAR (p<0.05), BINS10 (p<0.05), BINS20 (p<0.01)
AREA	N, YEAR	NS	-----	RANGE (p<0.001), MID75 (p<0.05), BINS10 (p<0.05), BINS20 (p<0.01), D20 (p<0.05)
AREA	N, CUTDEN, RORDER	NS	-----	RANGE (p<0.0001), MID75 (p<0.05), BINS10 (p<0.01), BINS20 (p<0.05)
AREA	BASIN, RORDER	p<0.05	ALL	RANGE (p<0.001), BINS10 (p<0.05), BINS20 (p<0.01)
AREA	N, YEAR, BASIN	p<0.001	MOST	RANGE (p<0.05), BINS10 (p<0.01), BINS20 (p<0.01)
RORDER	None	p<0.05	-----	D10 (p<0.01), SIMPD10 (p<0.01), SWH10 (p<0.05), EUQFQ1 (p<0.01)
RORDER	N, YEAR	NS	-----	BINS10 (p<0.05) ⁴ , SIMPD10 (p<0.01), EUQFQ1 (p<0.05)
RORDER	N, AREA, CUTDEN	NS	-----	BINS10 (p<0.05), D10 (p<0.01), D20 (p<0.05), SIMPD10 (p<0.001), SWH10 (p<0.05)
RORDER	N, CUTDEN	NS	-----	BINS10 (p<0.05), SIMPD10 (p<0.01), SWH10 (p<0.05), EUQFQ1 (p<0.05)
RORDER	N, BASIN	p<0.01	ALL	SIMPD10 (p<0.01), EUQFQ1 (p<0.01), EUQFQ23 (p<0.05)
RORDER	CUTDEN, BASIN	NS	-----	EUQFQ23 (p<0.05)
BASIN	None	p<0.0001	-----	BINS10 (p<0.01), BINS20 (p<0.01), D10 (p<0.05), SWH10 (p<0.05)
BASIN	N, YEAR	p<0.001	ALL	BINS10 (p<0.001), BINS20 (p<0.05), SWH10 (p<0.05)
BASIN	N, YEAR, CUTDEN	p<0.0001	ALL	BINS10 (p<0.01), BINS20 (p<0.05), SWH10 (p<0.05)
BASIN	N, YEAR, AREA	p<0.05	ALL	None
BASIN	N, RORDER	p<0.0001	ALL	BINS10 (p<0.001), BINS20 (p<0.01), SWH10 (p<0.05)
BASIN	RORDER, CUTDEN	NS	-----	KURT (p<0.05) ⁴

Table 4 (continued). Summary of regression analyses for environmental variables AREA, RORDER, BASIN, CUTDEN.

		Multivariate		Univariate
Variable	Covariates in Model	Significance of Variable ¹	Interaction Variables Significant ²	Size Metrics Univariate Significant for Variable ³
CUTDEN	None	p<0.0001	-----	MEAN (p<0.0001), MEDIAN (p<0.001), MID75 (p<0.0001), BINS10 (p<0.05), D20 (p<0.01)
CUTDEN	N, YEAR	NS	-----	MEAN (p<0.001), MEDIAN (p<0.01), RANGE (p<0.05), MID75 (p<0.01), BINS10 (p<0.01) ⁴ , BINS20 (p<0.01), D20 (p<0.01), SIMPD10 (p<0.05), SWH10(p<0.05) ⁴
CUTDEN	N, RORDER	NS	-----	MEAN (p<0.0001), MID75 (p<0.0001) ⁴ , BINS10 (p<0.05), EUQFQ1 (p<0.05) ⁴
CUTDEN	N, AREA	p<0.01	N (p<0.001)	MEAN (p<0.05), MID75 (p<0.05)
CUTDEN	N, BASIN	NS	-----	MEAN (p<0.05), MEDIAN (p<0.05) ⁴ , MID75 (p<0.01) ⁴ , BINS10 (p<0.05), BINS20 (p<0.01)
CUTDEN	BASIN, RORDER	NS	-----	MEAN (p<0.0001) ⁴ , MEDIAN (p<0.001) ⁴ , MID75 (p<0.0001), SKEW (p<0.05) ⁴

¹ NS = Not significant

² only if multivariate model was significant for variable

³ only if overall univariate model was significant; significant models where only interaction terms were significant are not reported

⁴ interaction terms also significant

Table 5a. Correlations (r) between spread metrics of size structure.

Metric	VAR	MID75	RANGE
VAR	1.00		
MID75	0.70	1.00	
RANGE	0.80	0.42	1.00

Table 5b. Correlations (r) between shape metrics of size structure.

Metric	KURT	SKEW	MODES
KURT	1.00		
SKEW	0.70	1.00	
MODES	-0.35	-0.17	1.00

Table 5c. Correlations (r) between diversity metrics of size structure.

Metric	BINS10	BINS20	D10	D20	SIMPD10	SWH10
BINS10	1.00					
BINS20	0.89	1.00				
D10	0.53	0.52	1.00			
D20	0.15	0.26	0.87	1.00		
SIMPD10	-0.70	-0.58	-0.52	-0.24	1.00	
SWH10	0.79	0.65	0.54	0.23	-0.94	1.00

Table 5d. Correlations (r) between size structure metrics across qualitative characteristics.

Metric	MEAN	MID75	RANGE	SKEW	MODES	BINS10	D20	SIMPD10	EUQFQ1
MEAN	1.00								
MID75	0.20	1.00							
RANGE	0.02	0.41	1.00						
SKEW	-0.54	-0.01	0.33	1.00					
MODES	-0.15	-0.15	-0.07	-0.02	1.00				
BINS10	0.13	0.12	0.74	0.14	0.02	1.00			
D20	0.18	0.24	0.17	-0.09	-0.16	0.15	1.00		
SIMPD10	-0.50	-0.11	-0.36	0.30	-0.15	-0.70	-0.24	1.00	
EUQFQ1	-0.21	0.15	-0.21	0.17	0.08	-0.52	-0.13	0.77	1.00

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